Icy insights from emperor penguins

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Almost 100 years ago, 3 stalwart members of Scott's Polar Expedition marched into the darkness of the Antarctic winter on what would become known as *The Worst Journey in the World* (1). Their goal was to recover the eggs of emperor penguins whose embryos might reveal important insights about the now-defunct theory that ontogeny recapitulates phylogeny. The men walked 108 km in temperatures as cold as −60 °C to reach the eggs, just as emperor penguins have done for millennia. Although 3 preserved eggs survived the journey, British embryologists dismissed their evolutionary insights. In this issue of PNAS, Jenouvrier *et al.* (2) reveal another kind of insight from emperor penguins: the population consequences of changes in sea ice that might forecast the fates of dozens of other species in the coming century.

Emperor penguins journey from the Antarctic oceans where they forage to breeding colonies on the landfast ice. There, they court, mate, and produce a single egg, which male penguins incubate on their feet for most of the 2-month gestation. Females journey back to the ocean to forage, returning to regurgitate seafood just as the hungry chicks hatch. In the ensuing weeks, both parents make multiple trips to the ocean to feed their growing chicks which, ideally, fledge as the melting ice edge approaches the breeding colony and food abundance peaks in the austral summer (3).

The success of the emperors appears to be critically dependent on the extent of the sea ice. When there is too much ice, hatching success declines (4), perhaps because females take too long to journey to and from the ocean and males abandon their eggs to save themselves from starvation. When there is little ice, adult mortality increases (4), perhaps because declining sea ice reduces the production of krill (5), which is the keystone of the Antarctic food web for emperors and many other species (6). The reason why krill depend on sea ice is not fully understood (5). One possibility is that melting glaciers reduce the salinity of seawater to favor smaller cryptophytes over larger diatoms in the phytoplankton community, causing a shift from krill to less nutritious salps in the zooplankton (7).

The relationship emperors exhibit between population success and sea ice (4) is also exhibited by other seabirds (8)

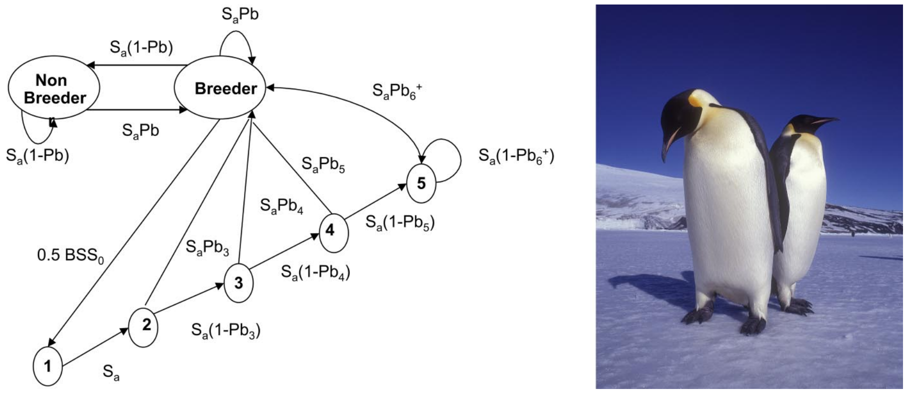

Fig. 1. Life cycle for emperor penguins at Terre Adélie, Antarctica. Survival probability is S_i for stage *i*. Minimum age at first breeding was 3 years; once recruited, birds reproduce annually with probability $S_a P_b$, where P_b is the proportion of breeders. BS is overall breeding success. Translation of this life cycle into a population projection matrix was described by Jenouvrier *et al.* (13). In the current article, Jenouvrier *et al.* (2) link past demographic responses to warm years to IPCC models of projected climate change to predict a persistent decline in the emperor penguin population at Terre Adélie and a 36% likelihood of extinction by 2100. Photo of emperor penguins reproduced with permission from ref. 13 (Copyright 2005, Ecological Society of America). Population model from Jenouvrier *et al.* (13).

and several marine mammals (9, 10). Although the sign and magnitude of these relationships varies among species (8), changes in sea ice extent are typically linked to prevailing sea surface temperatures, which are determined by patterns of global circulation. In the Antarctic, the Southern Oscillation produced an unusually warm year each 5 or 6 years through much of the last century (11), but climate change appears to be increasing the frequency, duration, and magnitude of warm phases in this and other oscillations (12).

The ubiquity of climate-mediated changes to marine food webs and the extraordinary time series of breeding data available for emperor penguins (4) give this new model by Jenouvrier the potential for far-reaching insights. The authors combined what is known about past responses by emperor penguins to variation in sea ice extent with projections about global climate to predict the future of the colony at Terre Adélie (2) (Fig. 1). They obtained climate forecasts from 10 Intergovernmental Panel on Climate Change (IPCC) models, categorized each into a series of warm and normal years based on various sea ice thresholds, and then modeled stochastic population projections based on the frequency of warm year events. The results indicate precipitous declines in the population by 2100 with a 36% likelihood of extinction.

The analyses (2) hinge on extrapolating the consequences for emperor penguins of a regime shift that occurred between 1972 and 1981, a period with unusually low sea ice extent that corresponded to a 50% decline in the emperor penguin population at Terre Adélie (2, 4). Jenouvrier *et al.* use this period to categorize the time series of emperor penguin reproduction into normal and warm years and then identify the thresholds at which deviations from normal could generate the same frequency of warm years (10 of 56 years or 18%) in the IPCC models. The standardized deviations needed to produce this frequency of warm years ranged from tiny (2%) to substantial (32%), but all of the models predicted increasing frequency of warm years and concomitant decreases in sea ice extent.

Comparable to their previous work (13), Jenouvrier *et al.* (2) used two projection matrices for their population model, each with 5 prereproductive age classes as well as breeding and nonbreeding adults. The model employs field data from a near-annual record that began in 1952, balancing details in

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vital rates against the sampling error inherent in such data. Without this remarkable long-term dataset the authors would not have been able to estimate all of the vital rates necessary for their demographic projections—previous attempts at population viability analysis have been criticized for failing to consider sampling error (14, 15). Although the model assumes that cohorts diminish in size only by mortality, and that any individual in the population could theoretically live "forever," senescence is functionally contained in the adult survival term of the model with no real consequences for population dynamics.

These population projections for penguins are realistic. The 10 IPCC models, which span a 200-year period between 1900 and 2100, were selected to match the actual surface ice information measured by satellites (2) in the actual foraging area used by the penguins (16). There is little doubt that the world will warm for emperor penguins and sea ice will diminish. Moreover, the models are based on the demographic responses of emperors to the warming that occurred in the 1970s; future warming events are predicted to be more extreme with, presumably, even more pronounced effects on Antarctic food webs.

Notwithstanding the considerable strengths of this work, there are a couple of limitations. First, the projection

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relies on the prediction of climate for 100 years. Ecologists and meteorologists are notoriously poor at predicting the future. An accumulation of estimation errors makes projections increasingly tenuous in the distant future, highlighting the importance of ongoing monitoring of population responses to current climate conditions (17). A second limitation is the binary depiction used to categorize the variability of temperature and sea ice extent into warm and normal years. Although this is a helpful simplification for population modeling, both sea surface temperatures and sea ice extent vary continuously and a categorical response to them may not be realistic.

In sum, the authors use an extraordinary time series to provide what may be the best example to date of a prediction of population trends based on climate projections. Their model paints a chilling picture for the future of emperor penguins. The next step will be to elucidate the mechanisms that link sea ice extent and population declines. Such understanding is needed if ecologists are to predict the diverse and paradoxical effects of climate change (17). In the southern oceans, those mechanisms likely hinge on krill productivity (5, 7) cascading through entire food chains. Emperors, near the top of the food chain, are likely foreshadowing the fates of dozens of other Antarctic species (8). Although these primitive birds did not reveal much about phylogeny 100 years ago, breeding records over half of the ensuing century have made them excellent harbingers of the ecological effects of climate change to come.

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